Developmental pathway, speciation and supraspecific taxonomy in amphibians
1. Why are there so many frog species in Sri Lanka?

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Sri Lanka (and probably also southern India) harbours an unusually high number of frog species, especially of the direct-developing rhacophorid genus *Philautus*. An hypothesis is proposed to try and account for the exceptional radiation in these frogs: these direct-developers would be submitted to "familial", rather than "individual", mortality, which could tend to increase allele fixation in isolated populations. Possible ways of testing this hypothesis, which is neither supported nor rejected by meta-taxonomic data (mean number of species per genus), are discussed. If confirmed, this hypothesis could account, at least in part, for some rapid and massive evolutionary radiations in some zoological groups, like cichlid fishes, birds and mammals.

Introduction

Several recent publications have pointed out the discovery that many new species of frogs remain to be described in Sri Lanka (Dutta & Manamendra-Arachchi, 1996, Pethiyagoda & Manamendra-Arachchi, 1998, Meegaskumbura et al., 2002*a-b*, Pennisi, 2002; Bossuyt et al , 2004) and probably also in southern India, especially in the Western Ghats (Biju, 2002) If confirmed, these findings would mean much more than double the number of frog species in Sri Lanka, and increase significantly the number of amphibian species in India. Most of these new species are members of the genus *Philautus* Gistel. 1848, a group of small tree-frogs belonging, according to the taxonomy adopted, either to the subfamily Rhacophorinae of the Ranidae (Dubois, 1992, Bossuyt & Dubois, 2001) or to the family Rhacophoridae (Vences & Glaw, 2001; Wilkinson, 2003) These frogs lay egg clutches in terrestrial shelters (in leaf litter, under stones or barks, etc.), where these large unpigmented eggs undergo direct development.

The information so far published on these findings is quite insufficient and unsatisfactory The only hard data available are cladograms based on genetic sequences in 57 "species" from Sri Lanka and neighbouring areas (MEEGASKUMBURA et al., 2002a; BOSSUYT et al., 2004) These molecular data are not to be found in the papers themselves, but in "Supporting online material" (SOM) which most readers are unlikely to ever see (see DUBOIS, 2003d). More importantly, the "new species" are yet to be properly compared (not only from a molecular point of view, but also in morphology, behaviour, bioacoustics, etc.), diagnosed, described and named, and the genus *Philautus* as a whole is still in bad need of a taxonomic revision (DUBOIS, 2004a). However, despite the paucity of genuine scientific evidence, the high number of undescribed species in Sri Lanka and southern India is certain. Pending a serious generic revision of the Sri Lankan and Indian rhacophorines, and the proper description of the unnamed species, we have to face the fact that Sri Lanka currently harbours more than five times more frog species than had been believed by former authors (e.g. GÜNTHER, 1864; BOULENGER, 1890; KIRTISINGHE, 1957; DUTTA & MANAMENDRA-ARACHCHI, 1996), and that probably many more species were present there still one century ago, before the massive deforestation of this island in the 20th century (PETHIYAGODA & MANAMENDRA-ARACHCHI, 1998; BAHIR et al., 2002). A similar, although perhaps less extreme, trend also no doubt exists in southern India, especially in the Western Ghats (BIJU, 2002) These two regions (Sri Lanka and the Western Ghats) have long been considered a single biodiversity region and hotspot, although they show important faunal differences and should rather be considered two distinct hotspots (BOSSUYT et al., 2004).

The discovery that Sri Lanka harbours a batrachofauna much richer than most other ones in the world, including in various other tropical regions, and possibly richer than any of them (see PETHIYAGODA & MANAMENDRA-ARACHCHI, 1998, 4), is puzzling, as highlighted by the journal *Science* (PENNISI, 2002). The comments on this finding published by this journal, however, are disappointing, as they do not suggest a serious scientific hypothesis to try and account for this fact. MEEGASKUMBURA et al. (2002a) simply wrote in this respect, "the persistence of so many species is striking and may be attributable to a combination of terrestrial eggs, direct-developing embryos, and high fecundity (up to 91 ova per clutch)". How a combination of these three "factors" might explain the unusual high number of frog species of this region remains a mystery Most of the comments from "experts" provided by *Science* (PENNISI, 2002) on this discovery are not more enlightening regarding the question "Why are there so many frog species in Sri Lanka?", a single one being relevant in this respect. "[Their] water-free lifestyle 'gives species a lot more latitude,' McDiarmid explains, and 'lends itself to geographic isolation and speciation" (PENNISI, 2002: 341). This suggests that terrestrial direct-development might favour speciation through [ecological] "latitude" and "geographic isolation", but evidence for these two suggestions, and even a detailed explanation of "how it could work", are wanting

To the best of my knowledge, two alternative hypotheses trying to explain the high number of *Philautus* species in Sri Lanka have been published. Interestingly, they are quite opposite The first one (PETHIYAGODA & MANAMENDRA-ARACHCHI, 1998, 4) relies on the restricted dispersion abilities of these frogs "a feature remarkable among the Sri Lankan Rhacophoridae is the exceedingly small range of distribution of many species, often less than 0.5 km² (.) Das (in litt.) suggests that the high diversity observed might be in part attributable to their reproductive mode (direct development), which probably restricts their

dispersion, unlike in species with aquatic eggs or larvae, which could disperse with flooding or flowing water (high diversity and local endemicity are also observed in the Neotropical frogs of the genus *Eleutherodactylus* (Leptodactylidae), many of which breed in phytothelms)." The second hypothesis, co-signed by the same authors (MEEGASKUMBURA et al., 2002b 12), states exactly the contrary. "It appears that direct-developing species have the potential to undergo rapid adaptive radiation in part through being independent of aquatic habitats, permitting their dispersal throughout the available expanse of humid-forest."

As a rule, breeding *Philautus* populations seem to be quite small (much smaller, at least, than populations of most frog species in open habitats) and tend to have strongly patchy distributions, with groups of males calling in bunches of close bushes, separated by large areas without calling males (repeated personal observations in forests of Sri Lanka, southern India, Nepal, Thailand and Yunnan). Thus, these frogs are not uniformly distributed on the forest floor. However, in this genus virtually nothing is known on the population size, distribution, behaviour and dispersal of non-breeding individuals, in particular of imagos. The fact that these frogs do not depend on water bodies for the deposition of their eggs would rather seem to speak for the absence of natural barriers between populations, which should rather be more liable than water-breeding species to meet and mix at breeding time in forested areas, but breeding populations appear to be rather isolated from each other and it is not known whether some individuals may disperse from one population to another and, if so, what are the quantitative parameters of such events (frequency, proportions of individuals involved, etc.). Pending detailed eco-ethological works on these frogs, which are currently wanting, the only possibility is to make general conjectures. Direct development probably plays a rôle in the observed phenomenon, associated with the small size, very limited range and semi-isolation, of many *Philautus* populations. It would seem that beside the possible, but yet precisely undocumented, limited population sizes and dispersion abilities of these frogs, another factor may play a significant rôle in their high speciation rate.

The present paper is devoted to the presentation of an hypothesis that could possibly account, at least in part, for the seemingly unexpected discovery and, of possible ways of testing this hypothesis. In a second related paper (DUBOIS, 2004c), comments are offered on related matters, in particular regarding amphibian generic taxonomy.

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1   An *imago* (Latin term meaning "image portrait", see DUBOIS 1978, 1997b) is a specimen similar in aspect to the adult, but smaller and sexually immature, which results either from metamorphosis (in species with tadpoles) or from hatching (in species which develop inside egg capsule). This term should be preferred to the term "metamorph", sometimes found in the literature for several reasons: (1) it has more generality, as it applies to species with "direct development" which do not show proper metamorphosis, but rather a continuous development from embryo to imago; (2) the term "metamorph" is unclear in meaning and confusing. This latter term has never been properly introduced into scientific literature as a new technical term but simply used, without formal definition, but then in three distinct senses: (a) to designate specimens during the process of metamorphosis, (2) to designate metamorphosed specimens as opposed to larvae, (3) to designate metamorphosed specimens as opposed to "neotenic" or "paedomorphic" ones, in species or genera that show both kinds of developments. Similarly, the anamhyotic adjective *imaginal* (derived from *imago*) should be used instead of the term "metamorphic" which is primarily an ecological term referring to metamorphism and whose use in zoology is confusing for the reasons mentioned above.

ARE THERE INDEED MORE FROG SPECIES IN SRI LANKA THAN ELSEWHERE?

Before discussing a possible hypothesis for the facts observed, the first question to ask is whether these facts are indeed exceptional. Although in the first part of the 20th century a number of biologists, including some zoologists, seemed to be confident that most of the living animal species of our planet had been discovered and named, except in a few "obscure" groups considered to be "of little interest", this idea is now completely abandoned. In the last decades, a number of studies have been devoted to this question and, although estimates are difficult and poorly reliable, it is now widely acknowledged that only a small proportion of these species have yet been recognized by zoologists: a conservative estimate in this respect is that, with about 1.75 million species currently recognized as "valid" by taxonomists (although not really "known", see DUBOIS, 2003c), the latter have only surveyed about 10 % of the total number of animal species still living on our planet, perhaps even much less (HAMMOND et al., 1995). This general estimate covers a very heterogeneous situation, as only a few groups of vertebrates (particularly the birds) can be considered "well surveyed", most higher taxa being "poorly" or "very poorly surveyed". Vertebrates as a whole are often considered to be "rather well surveyed", and, a few decades ago, many authors would have considered that this applies in particular to the living Amphibia, whose total number was believed to be rather low, a few thousands only. This was merely a reflect of the bad standard of amphibian taxonomy worldwide. In the second half of the 20th century, a strong increase in the number of known species followed the increase of field work in various parts of the planet, especially in tropical regions, and the introduction of new taxonomic concepts and methods (DUBOIS, 1998). As shown in table 1, the number of species recognized as valid by taxonomists has drastically increased in the last decades, and this trend should go on, at least as long as research positions and funds are available for this work, which is not certain (see DUBOIS, 1998, 2003c). Another way to realize how bad the amphibian species of our planet are known is to consider that, of 4536 amphibian species described by zoologists by the end of 2000, no less than 20.9 % were only known from a single locality, and only 75.8 % from more than two localities (tab. 2): had not a little more than 1000 localities been visited at least once, the number of amphibian species recognized by taxonomists would be one quarter lower than now. Furthermore, an important number of the species yet reported from a single locality (the type-locality) are currently known from a single specimen (the holotype); however, the sources used to compute the figures in tab. 1-2 are too incomplete to allow a reliable quantitative estimate in this respect.

In 2003, 5441 amphibian species were recognized (4761 Anura, 515 Urodela, 165 Gymnophiona), but, given the current rate of increase (tab. 1), it is reasonable to predict that zoologists have not yet collected, studied, described and named half of the amphibian species that still live on our planet, perhaps even much less, and since many of these species are currently threatened with extinction, a large proportion of them will probably disappear during our century before having been even encountered by man, or at least by taxonomists (DUBOIS, 1997a, 2001, 2003d).

Table . – Number of species of living amphibians considered valid by taxonomists at different dates, according to several checklists or checklist updates, and average rate of increase in this number per year during the history of amphibian taxonomy (see DUBOIS, 1987b: 101). The estimate for the year 2000 was obtained by adding the species reported in the *Zoological Record* as having been described as new from 1997 (GLAW et al. 1998) to the end of the year 2000. Date: last year covered by the checklist or the checklist update.

Date	Reference	Total number of species of Amphibia	Average yearly increase in species number since preceding date	Average proportional yearly increase since preceding date	Average yearly increase in species number since 1768	Average proportional yearly increase since 1768	Average yearly increase in species number since 1960	Average proportional yearly increase since 1960
1768	LAURENTI, 1768	57	—	—	—	—	—	—
1854	DUMÉRIL et al., 1854	734	2.06	3.61 %	2.06	3.61 %	—	—
1882	BOETTGER, 1882a,b	1003	27.46	11.74 %	8.30	14.56 %	—	—
1969	C. BURNAM, 1974	3343	26.90	2.68 %	16.35	28.68 %	—	—
1984	FROST, 1985	4015	44.80	1.14 %	18.32	32.14 %	44.80	1.34 %
1992	DUELLMAN, 1993	4522	63.38	1.58 %	19.93	34.96 %	51.26	1.53 %
1997	GLAW et al., 1998	4975	90.60	2.00 %	21.48	37.68 %	58.29	1.74 %
2000	This paper	5208	77.67	1.56 %	22.20	38.95 %	60.16	1.80 %
2003	DUELLMAN & SCHLAGER 2003	5441	77.67	1.49 %	22.91	40.19 %	61.71	1.85 %

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Table 2   Information on the number of localities from where 4536 amphibian species had been reported at the end of 2000. This table was computed from the same sources as in tab. 1, where the relevant data are lacking for many species, hence the total number of species lower than in tab. 1

Number of localities from which the species has been reported	Number of species	Percentage of species
A single locality (type-locality)	949	20 9 %
Type-locality and "vicinity", or two localities only	151	3 3 %
More than two localities	3436	75 8 %

Thus the question may be asked, whether the situation encountered in Sri Lanka (and possibly also in southern India) is indeed exceptional, or only results from the amphibian fauna of these areas having been particularly neglected until now, which is certainly true (DUBOIS, 1999, contra INGER, 1999). A tentative reply can be obtained by looking at some figures. According to GORHAM (1974), 3343 amphibian species were recognized as valid by taxonomists in 1969, and this number has raised to 5441 in 2003 (tab. 1), thus the increase over this 34-year period was of 2098 species, i.e. 62.8 % of the 1969 figure. The number of species occurring in Sri Lanka considered as valid by KIRTISINGHE (1957, followed by GORHAM, 1974) was 35; according to DUTTA & MANAMENDRA-ARACHCHI (1996), this number had risen to 53; now, according to PETHIYAGODA & MANAMENDRA-ARACHCHI (1998), the inclusion of the new species discovered in Sri Lanka before 2000 (but not yet described) is about 131, i.e. a increase of about 274.3 % of the 1969 figure over the 34-year period 1969-2003. Even if these figures are approximate and possibly exaggerated (but also possibly underestimated), it is quite clear that the *order of magnitude* in the increase of species is much higher in Sri Lanka than the average rate over the whole planet. A similar trend was identified in southern India (BIJU, 2002). A similar increase seems to have been observed in a single other region of the world, central and southern America, where a major contribution to this increase is due to the description of many new species of the genus *Eleutherodactylus* over the recent decades.

However, a strong increase in the number of recently discovered species has also been observed in other tropical regions of the world, and is therefore not by itself evidence that the total number of species of Sri Lanka and southern India is exceptionally higher. Evidence in this respect comes from a rough estimate of the number of known species per surface in a few "megadiversity" countries of the world, as presented by PETHIYAGODA & MANAMENDRA-ARACHCHI (1998) the species density per 1,000 km² was estimated as 0 06 in Brazil and India, 0 09 in Zaire, 0 13 in Indonesia, 0 22 in Venezuela, 0 36 in Colombia, 1 3 in Ecuador, 2 75 in Costa Rica and 3.9 in Sri Lanka Even if such estimates are not directly comparable, as they do not take into account various parameters that are likely to influence species diversity (such as latitude, altitude, climate or vegetation type), they also point to a difference in the *order of magnitude* in the number of species for a given surface between Sri Lanka (and southern India) and other tropical countries.

Another important consideration is that, of the 131 species estimated by PETHIYAGODA & MANAMENDRA-ARACHCHI (1998), 93 (i.e., 71 %) are reported to be "rhacophorid species", and that the vast majority of the latter are likely to be members of the genus *Philautus*, as

defined by DUBOIS (1987) and BOSSUYT & DUBOIS (2001a)². It is therefore very likely that the exceptional amphibian radiation observed in Sri Lanka is mostly, if not only, due to unusual species diversity in this genus, but not in all other genera, including endemic ones of Sri Lanka (*Adenomus, Lankanectes, Nannophrys*) (DUTTA & MANAMENDRA-ARACHCHI, 1996, MANAMENDRA-ARACHCHI & PETHOYAGODA, 1998, VENCES et al., 2000; DUBOIS & OHLER, 2001a). The situation is similar in southern India, at least in the Western Ghats (BIJU, 2002)

For the purpose of the present discussion, we will consider it very likely that Sri Lanka (and possibly southern India), mostly on account of the genus *Philautus*, just like central and southern America on account of the genus *Eleutherodactylus*, do indeed harbour exceptionally high numbers of amphibian species, many of which are very similar in aspect and have a very limited distribution, both factors that certainly contributed to the long underestimation of the number of frog species in these areas. If we consider this fact as most likely, what could be its explanation?

AN EVOLUTIONARY HYPOTHESIS

The vast majority of the new frogs recently discovered in Sri Lanka (and southern India) belong in a single genus, the tree-frog genus *Philautus* Gistel, 1848. As redefined by DUBOIS (1987, 1992) and reviewed by BOSSUYT & DUBOIS (2001), this genus now only includes direct-developing frogs. In frogs, "direct development", sometimes called "endotrophy" (e.g., McDIARMID & ALTIG, 1999), designates a mode of development that skips the usual free larval stage of anurans, the embryo's growth and differentiation being supported only by the resources that were available from the start within the envelopes of the egg, as vitelline reserves. In genus *Philautus*, such eggs are not deposited isolated, but as groups or "clutches" of eggs usually hidden under terrestrial shelters (under stones, leaf litter, tree barks, or in holes). During the whole development of the eggs, the latter remain together in this shelter; at hatching, the imagos leave the eggs and disperse on the ground and in the surrounding vegetation. The hypothesis proposed here is that these developmental particularities, by themselves, constitute particular ecological conditions likely to facilitate speciation, through a mode of mortality that is different from that usually encountered in frogs.

2 MEEGASKUMBURA et al. (2002) presented as a novelty the finding, shown in their molecular cladogram, that the Sri Lankan species usually referred to the rhacophorid genera *Theloderma* Tschudi, 1838 and *Rhacophorus* Kuhl & Van Hasselt, 1822 are not closely related to the other species of these two genera but are loosely related to those of the Sri Lankan species of the genus *Philautus*. This statement deliberately ignored several previous publications where the same hypothesis had already been proposed without any use of molecular data: thus, PETERS (1860), AHL (1931) and KIRTISINGHE (1957) had a ready placed the species *Pol_pedates schmarda* Kelaart 1854 (referred to *Theloderma* by LIEM, 1970, DUTTA & MANAMENDRA-ARACHCHI, 1996 and BOSSUYT & DUBOIS 2001) in the group now known as *Philautus* and DUBOIS (1987, 1992, 1999, BOSSUYT & DUBOIS, 2001) had already removed all Sri Lankan species placed by earlier authors in *Rhacophorus* from that genus, to place them in *Philautus*. Actually, maintaining these latter species in *Rhacophorus* (as done e.g. by DUTTA & MANAMENDRA-ARACHCHI 1996 and PETHIYAGODA & MANAMENDRA-ARACHCHI 1998) was already obsolete much before the *Science* paper (DUBOIS, 1999), and the latter should rather have stated that a *confirmed* the validity of this action rather than presenting it as new.

This hypothesis was already proposed earlier, as follows. "The particularities of intra- and interspecific variation in [the genus *Phlautus*] (intraspecific variability often higher than morphological differences between related species), where 'sibling' species (dualspecies) often have very different calls (personal observations in southern India), might be related to a particular mode of natural selection, connected with the reproductive and developmental modes of these species. As a matter of fact, in the species that lay numerous eggs in water, the tadpoles later disperse more or less, and are all submitted similarly to selection, which results in a roughly Gaussian distribution of characters in the population. In contrast, in *Phlautus* and in other groups with terrestrial clutches, containing a small number of eggs, the latter are certainly submitted to largely random but massive mortality: a given clutch, deposited by a female, runs the risk of being discovered by a predator, which can destroy it completely, but it can also remain undiscovered and reach safely overall eclosion." (DUBOIS, 1987: 71, translated).

For more clarity, we may consider an hypothetical and very simplified example. Let us compare the sympatric populations of two different frog species of the same size, having similar demographic conditions, i.e. a reproductive population of 5 males and 5 females, each female pairing with a single different male and laying 10 eggs, that will develop into 5 males and 5 females, and all adults dying after their reproduction. Let us further hypothesize that both populations are completely isolated, i.e. without immigration or emigration during the period considered. Species A lays its eggs in water, where they hatch after embryonic development, giving birth to tadpoles that spread in the water body, where they live randomly distributed, until they metamorphose into imagos. Species B lays eggs clutches under terrestrial shelters, where the eggs undergo direct development until they hatch as imagos. Let us now consider that, in both populations, mortality between egg-laying and the stage imago is 80 %, i.e., in both populations, 50 eggs are laid, 10 of which only reach the stage imago. Let us consider that this mortality is caused by predators, e.g. snakes. In population A, snakes will eat 40 tadpoles among the 50 randomly distributed in the pool, whereas in population B they will discover and eat 4 egg-clutches out of 5. It is quite clear that, if the only surviving clutch bears special characters, these will be widely distributed in the frogs resulting from this clutch, much more than in the population with tadpoles.

In some extreme situations, one generation may be enough to result in the total replacement of one allele by another in a population. This is the case e.g. if a mutation takes place in a sex-linked gene borne by the heterogametic chromosome, especially if this mutation occurs very early in the germ-line, ideally in the first primordial cell at the origin of the whole germ-line of an embryo. In anurans both male and female heterogamy do occur (DUELLMAN & TRUEB, 1985: 447, 450). The situation in *Phlautus* is unknown, but let us hypothesize that in this group, like in several global anuran ranids, the heterogametic sex is male (XY/XX type). If a mutation m occurs in the Y chromosome of the first primordial cell of an early embryo, all spermatozoa resulting from the divisions of this cell and bearing the Y chromosome (i.e., half of the spermatozoa of this individual) will bear the m allele, and all males resulting from fertilization of eggs by these spermatozoa will bear the mutation m. So, among our 5 hypothetical females, one will produce 10 embryos, all 5 males of which will bear m, whereas the 20 males produced by the other nine females will not. Now, under the schematic model developed above, the fate of the 5 m-bearing males will be very different in the two species. In the species with tadpoles, mortality among the 25 males will be random, and the probability

that the 5 surviving tadpoles bear m will be $5/25 \times 4/24 \times 3/23 \times 2/22 \times 1/21 = 120/6,375,600 = 0.000019$: thus the complete fixation of m in one generation will be a very unlikely event. On the other hand, in the direct-developing species, the probability that the 5 surviving males be bearers of m will be $1/5 = 0.20$. Thus, in this very special case, a single generation could easily allow fixation of a mutation in a population in a direct-developing species, whereas the same event would be very unlikely in a tadpole-developing species. As it is known that, in some cases, speciation can result from a single mutation in a single locus (see references and discussion in DUBOIS, 1988: 42), it is obvious that, in this example, speciation could be facilitated by the mode of mortality, which may be qualified of "familial" in direct-developing frogs, vs. "individual" in species with tadpoles.

Of course, this example is very schematic and simplistic, as the same result would not be obtained if an autosomic or homogametic sex chromosome was involved, in this case, even with the same demographic figures, several generations would be needed to result in the fixation of a new allele in the population, and then many other factors would interfere, such as population effective breeding size, population range, dispersal (immigration and emigration), longevity, "selective values" of the initial allele and of the mutation m, etc. Many models could be computed using various values for all these parameters, but they would be of little interest as long as we do not have more information on the actual values of these parameters in the populations of frogs considered. It is clear, however, that familial predation on all eggs of a female at once (or survival of all these eggs altogether) entails different results from random mortality of individuals in a mixed population. Could this factor explain the seemingly higher speciation rate in Sri Lankan *Philautus* than in other frog groups? There are several ways to test this hypothesis. One is to have a look at some metataxonomic data (as defined by DUBOIS & OHLER, 2001).

DEVELOPMENTAL MODE AND SPECIATION IN FROGS

Early anuran development can follow several rather different pathways (see e.g. McDIARMID & ALTIG, 1999). A majority of anuran species have free aquatic tadpoles that are "exotroph", i.e. that feed on bacterial, vegetal or animal resources found in the aquatic environment where they live. As this mode of feeding requires a behavioural and energetic investment for foraging, it can also be called *ergotrophy* (from the Greek *ergon*, "work"). The transition from the egg-enclosed embryo to the imago through such a free larval stage with active feeding is widespread, dominant and probably plesiomorphic in amphibians (but see BOGART, 1981), whereas other developmental modes are all apomorphic relative to the former. These derived modes of development are often collectively designated as "endotrophy" (e.g., THIBAUDEAU & ALTIG, 1999), which is incorrect as in some of them only the feeding is really internal (inside the egg), whereas in some others it comes from the parent or from brothers and sisters, i.e. from outside the egg (although inside one of the parents). It seems better to use the unambiguous term *lecithotrophy* (WOURMS, 1981) for feeding only upon the internal vitelline resources of the egg. For the more general category of all developmental modes that are not dependent from foraging for external feeding, I propose the new term *argiotrophy* (from the Greek *argia*, "idleness, inaction"). This category includes

species whose development takes place either within the genital tract or another pouch in one of the parents, or within the egg capsules, the eggs being deposited in some terrestrial or arboreal shelter. As discussed in more detail in a second paper (DUBOIS, 2004*c*), this category is heterogeneous as far as developmental pathways are concerned, but from an ecological point of view and for the purpose of the present discussion, it is a relevant category, as in all these cases the following conditions are met: all eggs of a clutch remain together during a large portion of their development, either as a clutch hidden in some shelter, or kept within the adult, during all this part of their development, these eggs are likely to be either discovered and destroyed altogether, or to remain undiscovered and safe. Thus all these cases are submitted to familial, not to individual, mortality.

The development of many species of anurans being still unknown, no complete review of the two major ecological categories of frogs regarding developmental mode is possible for the time being, but the information available, as gathered by ALTIG & MCDIARMID (1999), is presented in table 3. The taxonomy of amphibians being in constant change, the precise figures of such a table are bound to be obsolete before being published, but the general trends are likely to remain the same, at least for a few years. To prepare this table, a taxonomy slightly modified from the list in DUELLMAN & SCHLAGER (2003: 456-484) was followed[3], and each anuran genus was referred to either of four ecological categories, defined as follows: (T) genera known to have free aquatic tadpoles (at least briefly described in at least one species), (A) genera known to have another mode of development (argotrophy), without free aquatic tadpoles (at least briefly described in at least one species); (B) genera with both categories (among the species currently referred to the genus, at least one is known to have free aquatic tadpoles, and one to be argotroph); (U) unknown (the development of all species of the genus is currently unknown)

Information on the development is available for at least one species of 325 anuran genera. Among them, 227 genera (i.e., 69.8 °o) are known to have at least one species with free tadpoles but no reported argotroph species; 93 genera (i.e., 28.6 °o) are known to have an argotroph species but no reported species with free tadpoles; and only 5 genera (i.e. 1.5 °o) are considered to include both kinds of species.

The argotroph species are not randomly distributed among anurans. The latter are divided by a number of recent authors (e.g., SOKOL, 1977) in two groups or suborders, the Discoglossoidei and the Ranoidei[4]. Interestingly, argotrophy is much rarer in the Discoglossoidei, where it is known in 7 7 °o of the genera (2/26) against 30 2 °o (98/325) in the Ranoidei,

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[3] This list is unreliable for several groups, as some taxa appear twice in different parts of the classification (e.g., *Suncope* or *Ingerana bulu.uri*), some species are misplaced according to the classification chosen (e.g., in the genera *Hoplobatrachus*, *Limnonectes*, *Micophrys*, *Philautus* or *Rana*), some names (e.g., *Bombina*) are lacking altogether whereas others are listed as valid without explanation although they are currently considered junior subjective synonyms (e.g., in the genera *Amolops*, *Bufo*, *Limnonectes*, *Philautus* or *Rana*). Strangely enough, this list is not always consistent with the taxonomies presented for the families in the chapters of the book itself (HEICHAS et al., 2003). For example, in the Ranidae the information concerning several taxa (e.g., *Amolops*, *Elachyglossa*, *Eupeuso*, *Ingerana*, *Limnonectes*, *Occidozyga*, *Odorrana*, *Sphaerotheca* or *Stung.lopus*) are not compatible with those in the chapter devoted to this family (DUBOIS 2003*b*). In tables 3-4 here, the family Ranidae is understood as including the eleven subfamilies listed in the latter chapter as well as the subfamilies Mantellinae and Rhacophorinae. This conservative approach seems best until a robust phylogenetic hypothesis is agreed upon by many workers concerning the relationships between all these genera.
[4] These suborders are sometimes called (e.g., FELLER & HEDGES, 1998) Archaeobatrachia and Neobatrachia but these two names are invalid, being junior homonyms (DUBOIS 1984, 2004*b*)

Table 3 – Some data on the higher taxa (suborders and families) of anuran amphibians number of known genera and species (slightly modified from DUELLMAN & SCHLAGER, 2003, see note 3), developmental modes of genera (see text for details): T, ergotroph with free tadpoles; A, argiotroph, B, both argiotroph and ergotroph with free tadpoles developmental modes reported in genus; U, unknown.

Suborder	Family	Number of genera (and species)	Number of genera (and of species in these genera) with given developmental mode			
			T	A	B	U
Discoglossoidea	Ascaphidae	1 (2)	1 (2)	0	0	0
	Bombinatoridae	2 (10)	1 (8)	0	0	1 (2)
	Discoglossidae	2 (10)	2 (10)	0	0	0
	Leiopelmatidae	1 (4)	0	1 (4)	0	0
	Megophryidae	11 (127)	11 (127)	0	0	0
	Pelobatidae	3 (11)	3 (11)	0	0	0
	Pelodytidae	1 (3)	1 (3)	0	0	0
	Pipidae	5 (30)	4 (23)	0	1 (7)	0
	Rhinophrynidae	1 (1)	1 (1)	0	0	0
	Total	27 (198)	24 (185)	1 (4)	1 (7)	1 (2)
Ranoidea	Allophrynidae	1 (1)	0	0	0	1 (1)
	Arthroleptidae	6 (76)	4 (41)	2 (35)	0	0
	Brachycephalidae	1 (6)	0	1 (6)	0	0
	Bufonidae	35 (448)	16 (389)	15 (53)	0	4 (6)
	Centrolenidae	3 (136)	3 (136)	0	0	0
	Dendrobatidae	10 (201)	9 (98)	0	1 (103)	0
	Heleophrynidae	1 (6)	1 (6)	0	0	0
	Hemisotidae	1 (10)	1 (10)	0	0	0
	Hylidae	43 (823)	35 (736)	4 (31)	1 (46)	3 (10)
	Hyperoliidae	19 (248)	15 (243)	0	0	4 (5)
	Leptodactylidae	49 (1085)	33 (325)	13 (752)	1 (6)	2 (2)
	Limnodynastidae	10 (49)	8 (45)	2 (4)	0	0
	Microhylidae	66 (356)	27 (1 8)	36 (214)	0	4 (4)
	Myobatrachidae	13 (73)	6 (65)	5 (6)	0	2 (2)
	Ranidae	61 (1040)	45 (798)	11 (170)	1 (68)	4 (4)
	Rhinodermatidae	1 (2)	0	1 (2)	0	0
	Sooglossidae	2 (3)	0	2 (3)	0	0
	Total	323 (4563)	203 (3010)	92 (1296)	4 (223)	24 (34)
Total		350 (4761)	227 (3195)	93 300	5 230	25 36

a matter that should call future attention from the phylogenetic point of view. The only two genera of Discoglossoidei in which some species are reported to be argiotroph are *Pipa* Laurenti, 1768 (where embryos develop on the back of the female and rely on their vitelline reserves alone for development) and *Leiopelma*, with two different kinds of argiotrophy (with free non-feeding tadpoles in dorsal pouch of father and direct development within egg capsule). Besides, THIBAUDEAU & ALTIG (1999: 172) listed the Megophryidae among the families including at least one "endotroph" species, but this was based on a misidentification of direct-developing eggs of *Philautus aurifasciatus* (Schlegel, 1837) as *Xenophrys longipes* (Boulenger, 1885), a mistake corrected by LEONG & CHOU (1998).

In contrast, in the Ranoidei, a vast array of argiotroph developmental pathways have developed. The distribution of argiotrophy within the various families follows no clear or consistent pattern: this category is found in various groups that have no direct cladistic relationships, which suggests that these derived modes of development appeared independently in these groups and are therefore homoplasic. This was precisely documented in some cases only (MARMAYOU et al., 2000), but is very likely in several others. In a few cases however, retention of a silent "direct development program" in tadpole-developing species, or the reverse, probably occurred (see DUBOIS, 2004c).

Argiotroph species are reported only in 13 of the 20 families currently recognized in the Ranoidei. Among the 299 genera of Ranoidei for which information is available for at least one species, 203 (i.e., 67.9 %) are known to include only species with free aquatic tadpoles, 92 (i.e., 30.8 %) are known to include only argiotroph species, and 4 (i.e., 1.3 %) are considered to include both.

The hypothesis presented above is that taxa (genera, families) including species confronted with "familial" mortality would tend to have higher rates of speciation than taxa with species submitted to "individual" mortality. An empirical confirmation of this hypothesis would be provided if anuran genera including argiotroph species had a higher mean number of species than genera with free tadpoles. As a first apparent confirmation of this trend, the most speciose anuran genus is the direct-developing *Eleutherodactylus* Duméril & Bibron, 1841, which, with about 680 species known in 2003 (and perhaps as many yet to be discovered and described), is also the most speciose genus of all vertebrates. However, this trend is not confirmed over the whole group of anurans, at least in the current state of knowledge. Over the 325 anuran genera for which developmental data are available (tab. 3), the mean number ($x \pm s$) of included species is 14.1 ± 34.3 (range 1-326) for the 227 genera that include only species with free aquatic tadpoles, and 15.6 ± 69.9 (range 1-682) for the 98 genera that include at least one argiotroph species. The difference is not statistically significant (Mann-Whitney U test $U = 9776.5$, $P = 0.09$), but this is of little meaning as a large majority of the anuran genera include very few species. Table 4 gives the number of known species of the 43 most speciose genera of anurans (i.e., including more than 20 species), with their known modes of development: here also, the mean number of species is higher in the 10 genera including at least one argiotroph species (114.0 ± 201.3, range 22-682) than in the 33 genera known to include only species with free aquatic tadpoles (66.5 ± 69.4, range 21-326), but, given the large variance in each group, the difference is still not statistically significant (Mann-Whitney U test $U = 155$, $P = 0.77$)

Table 4.   Some data on the 43 genera of anurans with the highest numbers of species (from the same source as in table 3). Developmental modes of genera (see text for details); T, ergotroph with free tadpoles; A, argotroph; B, both argotroph and ergotroph with free tadpoles developmental modes reported in genus; U, unknown.

Rank	Family	Genus	Number of species	Developmental mode
1	Leptodactylidae	*Eleutherodactylus* Duméril & Bibron, 1841	682	A
2	Hylidae	*Hyla* Laurenti, 1768	326	T
3	Bufonidae	*Bufo* Laurenti, 1768	247	T
4	Ranidae	*Rana* Linnaeus, 1758	221	T
5	Hyperoliidae	*Hyperolius* Rapp, 1842	117	T
6	Hylidae	*Litoria* Tschudi, 1838	112	T
7	Dendrobatidae	*Colostethus* Cope, 1866	103	B
8	Hylidae	*Scinax* Wagler, 1830	87	T
9	Ranidae	*Philautus* Gistel, 1848	83	A
10	Bufonidae	*Atelopus* Duméril & Bibron, 1841	74	T
11	Ranidae	*Rhacophorus* Kuhl & Van Hasselt, 1822	69	T
11	Ranidae	*Phrynobatrachus* Günther, 1862	69	T
13	Ranidae	*Mantidactylus* Boulenger, 1895	68	B
14	Leptodactylidae	*Leptodactylus* Fitzinger, 1826	62	T
15	Centrolenidae	*Cochranella* Taylor, 1951	61	T
16	Ranidae	*Limnonectes* Fitzinger, 1843	53	T
17	Hyperoliidae	*Leptopelis* Günther, 1859	51	T
18	Ranidae	*Platymantis* Günther, 1859	50	A
19	Ranidae	*Boophis* Tschudi, 1838	47	T
19	Ranidae	*Ptychadena* Boulenger, 1917	47	T
19	Leptodactylidae	*Telmatobius* Wiegmann, 1835	47	T
22	Hylidae	*Gastrotheca* Fitzinger, 1843	46	B
23	Leptodactylidae	*Physalaemus* Fitzinger, 1826	45	T
24	Centrolenidae	*Centrolene* Jiménez de la Espada, 1872	40	T
25	Ranidae	*Amolops* Cope, 1865	36	T
26	Centrolenidae	*Hyalinobatrachium* Ruiz-Carranza & Lynch, 1991	35	T
27	Megophryidae	*Scutiger* Theobald, 1868	34	T
28	Dendrobatidae	*Dendrobates* Wagler, 1830	33	T
29	Hyperoliidae	*Afrixalus* Laurent, 1944	32	T
30	Leptodactylidae	*Phrynopus* Peters, 1874	31	A
31	Ranidae	*Odorrana* Fei, Ye & Huang, 1991	30	T
32	Microhylidae	*Cophixalus* Boettger, 1892	29	A
32	Dendrobatidae	*Epipedobates* Myers, 1987	29	T
32	Hylidae	*Phrynomedusa* Wagler, 1830	29	T
35	Ranidae	*Paa* Dubois, 1976	27	A
36	Microhylidae	*Oreophryne* Boettger, 1895	26	A
37	Leptodactylidae	*Cycloramphus* Tschudi, 1838	25	T
38	Microhylidae	*Microhyla* Tschudi, 1838	24	T
38	Hylidae	*Vitreorana* Steineger, 1916	24	T
38	Myobatrachidae	*Uperoleia* Gray, 1841	24	A
41	Arthroleptidae	*Schoutedenella* de Witte, 1921	22	A
42	Bufonidae	*Ansonia* Stoliczka, 1870	21	T
42	Megophryidae	*Megophrys* Kuhl & Van Hasselt, 1822	21	T

Such an empirical approach to this question has only a very limited value, for several reasons. First, the category of argiotrophy is ecologically rather homogeneous regarding the question here posed (at least, all species in this category are likely to be submitted to "familial" mortality during development), but rather heterogeneous in developmental terms, as discussed in more detail elsewhere (DUBOIS, 2004c). Information available on detailed developmental pathways is currently too scanty in most genera without free aquatic tadpoles to allow for a more detailed analysis. For the time being, data are insufficient to allow to test statistically the existence of significant differences regarding mean species numbers in genera having different developmental pathways within the ecological category of argiotrophy.

Second, comparison of the number of species per genus would make fully sense only if all taxonomists were using the same "genus concept". However, despite precise proposals in this respect (DUBOIS, 1988), there currently exists no consensus among zootaxonomists about "what is a genus", and there is no reason to think that the various genera of anurans are "equivalent" by any standard (for a detailed discussion of this concept of taxonomic equivalence, see DUBOIS, 1988: 59-67). Clearly, some genera (e.g., *Hyla*, *Mantidactylus* or *Rhacophorus*) are rather heterogeneous assemblages that will most likely be dismantled in the future, as was the case for *Rana* in the recent decades (see DUBOIS, 2003b). Others appear to be more homogeneous groups that may keep their status of genera in the future (e.g., most of the genus *Bufo*). This question also is tackled again in more detail elsewhere (DUBOIS, 2004c).

Another major problem comes from the fact that all genera have not been submitted to the same effort of work in the recent decades. A striking fact for all experienced taxonomists is that the taxonomy of some frog genera is more "difficult" than that of others, because they show both a large overall similarity between species and unusual patterns of variation (with some of the interspecific variation overlapping intraspecific variation). This no doubt has acted as a break against their recent taxonomic revision. Among such genera, although not alone, are some genera of argiotrophic species, such as *Philautus* mentioned above, or the African *Arthroleptis-Schoutedenella* complex. The possibility is strong that revision of such genera, using morpho-anatomical, molecular, bioacoustic and cytogenetic characters, might disclose the existence of many more species than is actually believed. For these reasons, this empirical approach does not allow to really test the evolutionary hypothesis presented above.

Finally, and perhaps more importantly, comparisons as made above are likely to be statistically invalid as they do not rely on phylogenetic information. To be significant, such comparisons should use cladograms as input or be made between sister-taxa, but the information available on the phylogenetic relationships between the 325 anuran genera considered above is too incomplete to be used in this analysis, and restricting the comparisons to the few groups of genera for which reliable cladistic data are available would not allow genuine statistical comparison as the numbers would be much too low. However, this question should be kept in mind for the future, and considered again when our understanding of phylogenetic relationships between anuran genera is well improved.

For the time being, there are other possible ways to test the hypothesis presented above. As suggested above, models utilizing various populational, ethological and ecological parameters could be devised to investigate the theoretical likeliness that argiotrophy might facilitate speciation in frogs.

Another approach would be through biological comparisons within couples of phylogenetically related sympatric species of similar size and natural histories (except developmental mode), one of which lays clutches of eggs that give birth to free aquatic tadpoles, whereas the other one has another developmental mode, either in some external shelter or in some pouch of one of the parents. Several parameters may be considered for such comparisons, such as genetic polymorphism, heterozygosity and "genetic variance", measured e.g with the F_{ST} fixation index of WRIGHT (1965), or also cytogenetic differentiation. If the hypothesis above is correct, argiotroph species should show a significant tendency to allele fixation in small isolated populations. This does not necessarily imply that they would show significantly different mean genetic polymorphisms or heterozygosities than species with free tadpoles, because if predation on clutches is random the net effect on allele frequencies will be zero over the course of successive generations. On the other hand, if the populations are indeed quite isolated and small, they would tend to show local genetic drift and genetic variance between them should be more important than between similar populations of species with free tadpoles.

Empirical data to support or refute this hypothesis are lacking, as until now argiotrophy does not seem to have been particularly discussed as a pertinent factor in speciation rate, genetic polymorphism and evolutionary patterns in amphibians. WRIGHT's (1951) theories on relationship between population characteristics and genetic structure would seem a good start for such works. This was the case in INGER et al (1974)'s study dealing with several populations of Malaysian bufonids and ranids: evidence was found for lower genetic variation in species with linear distribution along streams and breeding among neighbours than in species with large panmictic breeding aggregations. Unfortunately, this nice study was not followed by others in other areas, that would have allowed to increase the sample size and test the generality of these findings. More data are available in Urodela, but here also no study has yet focused on a detailed comparison between related and sympatric ergotroph and argiotroph species. In plethodontids, argiotroph taxa show great spatial heterogeneity and very high genetic variance between populations, although local heterozygosity may be relatively low (LARSON, 1984; LARSON et al., 1984b), which is congruent with the hypothesis presented above. The highest heterozygosities in argiotroph salamanders have been found in species with dense populations (HANKEN & WAKE, 1982; WAKE & YANEV, 1986; GARCÍA-PARIS et al., 2000). Particularly relevant for the present discussion is the recent study by CRAWFORD (2003) on mitochondrial and nuclear DNA variation in four Central American species of *Eleutherodactylus*, which showed considerable values of genetic variance between populations. This author also found very large effective population sizes in these species. Applying a molecular clock model, he concluded that the unusually high species diversity in the genus *Eleutherodactylus* was probably not due to higher speciation rate but to old age, and he suggested that "the tropics have functioned as a museum of antiquity rather than as a cradle of speciation" (CRAWFORD, 2003: 2537). However, whether the molecular clock model validly applies to these taxa remains open to question

As for cytogenetic differentiation, BOGART (1991) pointed out the importance of demonstrable karyotypic changes involving modification of chromosome number in the genus *Eleutherodactylus* He also remarked that karyotypic diversity seemed larger in "smaller genera that contain species with terrestrially developing or direct developing eggs" (BOGART, 1991 242), such as *Arthroleptis*, *Cardioglossa*, *Fritziana*, *Leptopelis* or dendrobatid genera In

such groups, major karyotypic changes would occur by centric fusion and fission in small, isolated populations where inbreeding would "fix mutational events in a homozygous condition" (BOGART, 1991. 254). This model would seem more difficult to apply to large populations.

Such kinds of comparative studies would be worth undertaking both in frogs and in salamanders. For more generality, such studies could be carried out in several taxonomic groups and in different regions and kinds of habitats of the world. To come back to the genus *Philautus*, which prompted this reflexion and has never been the matter of detailed demographic, ecological, genetic and cytogenetics studies, it would appear most crucial to develop such researches to try and throw more lights on its evolutionary patterns.

Should the hypothesis turn out to be supported, it could have far-reaching consequences. If "familial" mortality indeed facilitates speciation, this fact might explain in part the high rates of speciation and of evolution observed in some animal groups displaying parental care, such as the birds or the cichlid fishes (with their striking radiation in the great African lakes: see e.g. JOHNSON et al., 1996) or true viviparity, such as the mammals. Starting from other premises, other authors (e.g. WILSON et al., 1975, BUSH et al., 1977; WYLES et al., 1983; LARSON et al., 1984a, SAGE et al., 1984) already discussed the factors possibly involved in such cases of rapid speciation, and, although they insisted mostly on the rôle of chromosomal evolution and of social behaviour, their data are not incompatible with the present hypothesis. If the latter is correct, the unexpected high number of species of *Philautus* in Sri Lanka as compared with the number of frog species in other parts of the world would be accounted for by the fact that these Sri Lankan frogs *are not precisely frogs*, at least not usual frogs with aquatic eggs and larvae, but other "kinds" of animals. In fact, if one forgets the numerous *Philautus* species, the amphibian fauna of Sri Lanka does not appear in the least exceptional, rather it would seem poorer than those of other areas of similar latitude, even in the same part of the world. Is this because of competition with the unusually successful *Philautus* clade?

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